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REVIEW

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Screwed up: Spirality of segments and other iterated structures suggest an underlying principle of seriality in bilaterians

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Abstract

This review deals with helicomery, that is, the specific malformation of a spiral arrangement of segments and other serial structures. Helicomery was first described in annelid and arthropod body segments. However, corresponding patterns occur in arthropod appendages and other bilaterians with serially arranged body parts, such as tapeworms, nematodes, vertebrates, and probably chitons. The specifics of the spirals such as length, orientation, and handedness are described. Most spirals are dorsal and comprise only a few loops. Helicomery is formed by a shift of cells during development or in adults caused by changes in cell adhesion or mechanical impacts such as lesions. A model for the formation of helicomery is proposed, which is based on medieval church labyrinths. These complex spiral structures are derived from concentric lines by the shift of relatively few tiles. This principle of "small causes, great effect" also applies to "spiral segments," because helicomery dissolves segmental patterns and questions the concept of segments as distinct structures. The widespread occurrence of helicomery in nonhomologous serial structures might indirectly indicate an underlying principle of seriality among Bilateria.

KEYWORDS
Annelida, Arthropoda, Cestoda, helicomery, limbs

1 | INTRODUCTION

Morphological spirals are widespread among animals. There are planar spirals formed by the proboscis of butterflies, the trunk of elephants, and the shells of ammonites and nautilids (Kröger et al., 2011; Wagensberg, 2008). Three-dimensional spirals such as screws and helices occur as snail shells, the tusk of the narwhal, the horns of artiodactyls (Tarassow, 1999), and less obvious in the stomach of elasmobranchs, lungfish, and sturgeons (Hassanpour & Joss, 2009; Olsson, 2011), the taenidia of hexapod tracheae (Seifert, 1975; Webster et al., 2015), and the smooth musculature of the human ureter (Leonhardt, 1981). It is generally thought that spirals evolved as a means of saving space and better maneuverability (butterfly proboscis, ammonites, gastropod shells, spiral guts) (Kröger et al., 2011; Olsson, 2011; Wagensberg, 2008), but additional roles can be seen in a stabilizing effect (narwhal tusk, taenidia) and in transport (shark stomach, ureter; Leonhardt, 1981; Wilson & Castro, 2010). Often the effect of spirals is a combination of different roles. All of these spirals are the result of adaptation and internal forces, and are established in the genomes of the species that possess them. Here, I discuss another class of spirals that occurs only occasionally as a deformity, either naturally or as a result of experimental manipulations.

One of the most fascinating malformations of the trunk of various segmented animal groups is the occurrence of spiral segments or helicomery (derived from the Greek helix = spiral and meros = part, section; e.g., Bateson, 1894; Morgan, 1895; Fusco et al., 2008;

Scholtz, 2020a). Helicomery appears as a helical pattern of one or several segments, or more neutrally, serial body units, instead of the regular sequence of each segment being separated from the following segment by a proper segmental boundary circumscribing the entire body in parts of the trunk. Apart from the early comprehensive treatment of helicomery by Morgan (1895), many cases have been more or less anecdotally described in a number of arthropods and annelids. These reports are based on animals found in the wild or on the outcome of different experimental manipulations. The descriptions are mostly restricted to the external segmental or other serial structures of adult or larval specimens. Helicomery has been frequently described in the context of a number of different, but perhaps related, segmental malformations such as missing or additional half segments, partial fusions of adjacent segments, or incompletely fused hemisegments (e.g., Balazuc, 1948; Leśniewska et al., 2009; Morgan, 1895; Scholtz, 2020a). However, a spiral or screwed arrangement of serial structures is such a unique pattern that it deserves special treatment. The causes for this unusual pattern are not understood. Nevertheless, it seems evident that this malformation is related to regeneration and/or irregular embryonic differentiation. However, so far a comprehensive review is missing.

2 | ANNELID AND ARTHROPOD SEGMENTS

Helicomery was first observed in polychaete and cltellate annelids (Cori, 1892; Morgan, 1892, 1895; Buchanan, 1893; Storch, 1913; Sayles, 1936; Figure 1). In addition, it has been found in all major groups of arthropods: chelicerates (Ćurčić et al., 1983; Juberthie, 1968; Mattoni, 2005; Pedder, 1965), myriapods (Balazuc & Schubart, 1962; Brölemann, 1894, 1904; Demange, 1972; Demange & Pereira, 1980; Leśniewska et al., 2009; Minelli & Pasqual, 1986; Simaiakis et al., 2007), insects (Morgan, 1895; Cappe de Baillon, 1927; Cockayne, 1929, 1934; Balazuc, 1948, 1958; Ramsay, 1959; Benton & Jennings,1975; Hesse-Honegger, 1998; Chesebro, 2012; Ornosa et al., 2001; Pix, 2014; Popovici et al., 2014), and crustaceans (Keilbach, 1958; Linder, 1947, 1952; Longhurst, 1958; Morgan, 1895; Šaganović et al., 2019; Scholtz, 2020b) including pentastomids (Spencer, 1892, Heymons, 1931; Figures 2 and 3). There are even fossil examples of spiral segments as exemplified by Cambrian and Ordovician trilobites (Owen, 1985; Rudkin, 1985; Figures 2 and 3).

3 | WHAT ARE THE PATTERNS OF HELICOMERY?

Spiral segments mostly begin and end with an incomplete segmental ring that shows a loose end (Figures 1–3). However, the character of the loose ends of the spirals differs regarding the degree of separation or fusion with neighbor segments (Buchanan, 1893; Morgan, 1895) (Figures 1-3). The spirals can be right handed or left handed (Figures 1-3). In most descriptions, the loose ends are situated on the dorsal side and all 40 experimentally generated cases of helicomery in the opilionid *Odiellus troguloides* (Lucas, 1847) were of the dorsal type (Juberthie, 1968). In some cases, however, the loose ends were found

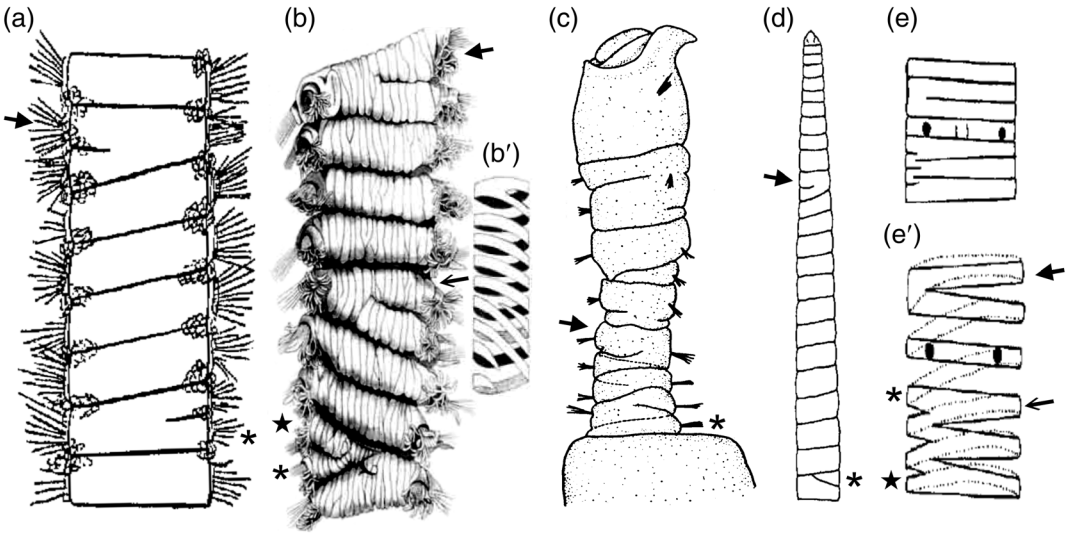

FIGURE 1 Spirals in Annelida. (a–c) "Polychaeta," (d-e′) Clitellata. (a). Errantia: *Amphinome* sp. Bruguière, 1789 dorsal view, right-handed spiral (after Morgan, 1895), (b,b′) Errantia: Drawing and scheme of *Amphinome* sp. dorsal view, two spirals: One in other, both left-handed, (after Buchanan, 1893). (c) *Sedentaria*: Regeneration of the anterior end of *Clymenella torquata* (Leidy, 1855) dorsal view, somewhat lateral in the anterior part, right-handed spiral (slightly different interpretation compared with that of Sayles, 1936) (after Sayles, 1936, with permission from University of Chicago Press), (d). "Oligochaeta": Anterior region of the earthworm *Eisenia fetida* (Savigny, 1826), dorsal view, right-handed spiral in segments 11 to 24 (after Morgan, 1895). (e, e′) Hirudinea: *Macrobdella decora* (Say, 1824) ventral view, two left-handed spirals (after Morgan, 1895). In all images, the beginning of the spiral is marked with an arrow, the end with an asterisk. If there are two spirals, the beginning of the second spiral is marked with a slim arrow and the end with a star

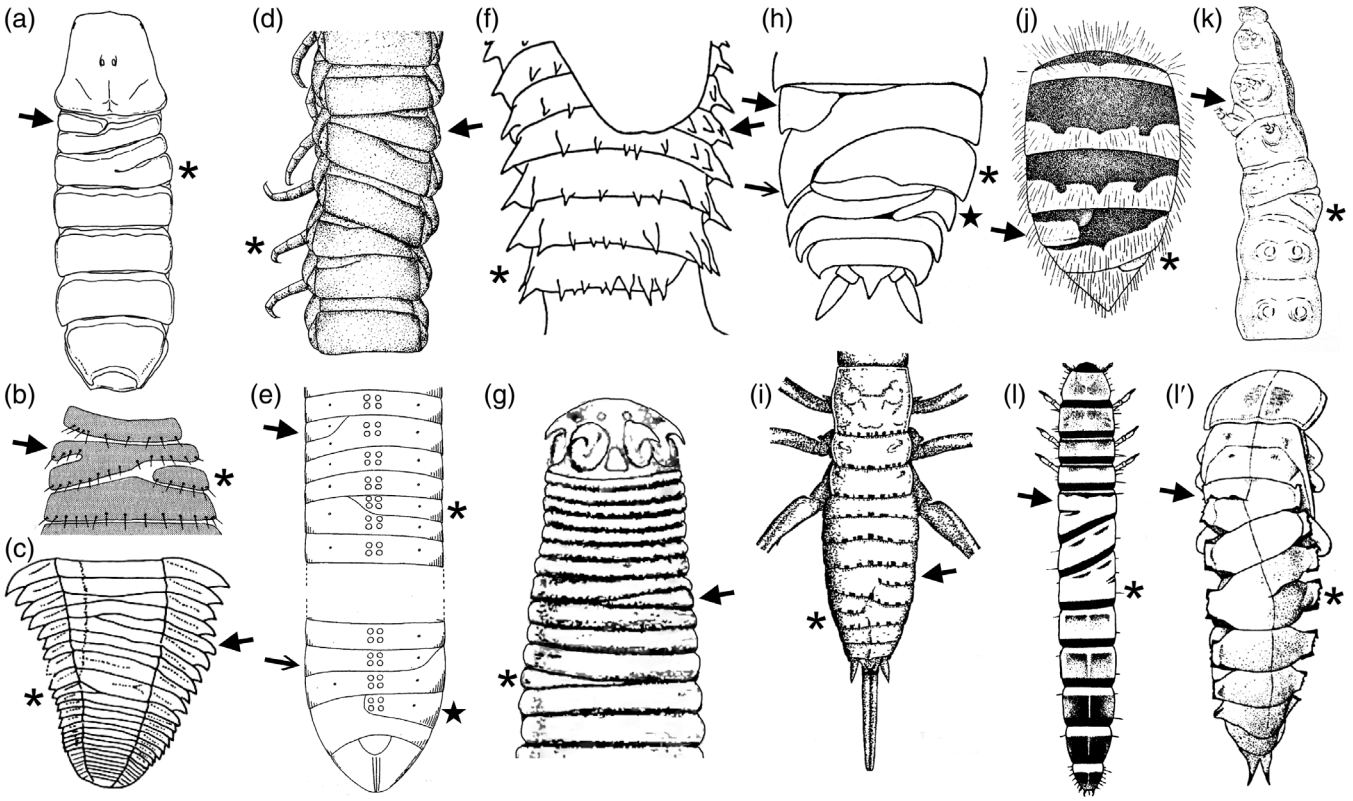

FIGURE 2 Spirals in Arthropoda. (a), (b) Chelicerata, (c) Trilobita, (d, e) Myriapoda, (f–h) "Crustacea," (i–l′) Hexapoda. (a) Scorpiones: *Brachistosternus roigalsinai* Ojanguren-Affilastro, 2002 dorsal view, right-handed spiral in the opisthosoma (after Mattoni, 2005, with permission from the author). (b). Pseudoscorpiones: *Neobisium fuscimanum* (C.L. Koch, 1843) dorsal view, right-handed spiral in the opisthosoma. (after Ćurčić et al., 1983, with permission), (c) Trilobita: Cambrian *Emuella polymera* Pocock, 1970, dorsal view, left-handed spiral in the thorax (after Owen, 1985, with permission from Cambridge University Press). (d) Chilopoda: *Stigmatogaster subterranea* (Shaw, 1794), dorsal view, left-handed spiral in the trunk (after Leśniewska et al., 2009, with permission from Elsevier). (e). Diplopoda: *Neptunobolus hogei* Schubart, 1949, ventral view, two right-handed spirals of diplosegments (after Balazuc & Schubart, 1962, with permission from Elsevier). (f). Notostraca: *Lepidurus lynchi* Linder, 1952, ventral view, left-handed spiral in the abdomen (after Linder, 1952). (g). Pentastomida: *Waddycephalus teretiusculus* (Baird, 1862) ventral view, left-handed spiral in the trunk (after Spencer, 1892). (h). Isopoda: *Porcellio scaber* Latreille, 1804 dorsal view, two right-handed spirals: One in the thorax, one in the pleon (after Keilbach, 1958, with permission from Elsevier). (i) Orthoptera: *Deinacrida carinata* Salmon, 1950, dorsal view, left-handed spiral in the abdomen (after Ramsay, 1959, with permission from the Royal Society of New Zealand), (j) Hymenoptera: *Dolichovespula sylvestris* (Scopoli, 1763) dorsal view, right-handed spiral in the abdomen, (after Cockayne, 1934, with permission from Wiley. (k) Lepidoptera: Larva of *Lacanobia suasa* (Denis & Schiffermüller, 1775), ventral view, right-handed spiral passing the boundary between thorax and abdomen (after Cockayne, 1934, with permission from Wiley). (l, l′) Coleoptera: Larva and pupa of *Tenebrio molitor* Linnaeus, 1758, dorsal view, right-handed spiral in the abdomen, (after Balazuc, 1948, with permission from Muséum national d'histoire naturelle, Paris). In all images, the beginning of the spiral is marked with an arrow, the end with an asterisk. If there are two spirals, the beginning of the second spiral is marked with a slim arrow and the end with a star

on the ventral side and only rarely laterally (see Morgan, 1895) (Figures 1-3). Ventral helicomery is characterized by a pattern, in which ventral serial structures that belong to a dorsal "segment" are not connected ventrally (Figure 2k). Dorsal helicomery shows dorsal serial structures that are not connected, but belong to one ventral "segment" (Figure 2h). Spirals have been found in the middle of the body and in proximity to the terminal regions. In arthropods they can cross tagma boundaries as has been demonstrated in the moth *Tineola bisselliella*, in which a spiral runs from the thorax to the anterior abdominal segments (Lüscher, 1944) (Figure 2k).

Helicomery can comprise one to several turns. The longest spiral found in annelids comprised twelve and a half turns (Morgan, 1895) (Figure 1d), the longest spiral in insects consisted of six turns (Balazuc, 1948), and in notostracan crustaceans of a little more than four complete turns (Linder, 1952). Yet, shorter spirals are more frequent (Balazuc, 1948; Juberthie, 1968; Linder, 1952; Morgan, 1895). Sometimes more than one region of spiral segmentation has been found in one animal, as has been observed in annelids (Morgan, 1895; Sayles, 1936) and arthropods (Balazuc, 1948; Linder, 1952; Figures 1 and 2). In addition, Buchanan (1893) described a case of two concurrent spirals that form a double helix in a polychaete (Figure 1b,b′).

Most available descriptions of helicomery deal with external aspects. In contrast to this, information regarding internal structures is scarce. Morgan (1895) described the arrangement of ganglia, nephridia, and segmental coelomic cavities in spiral segments of earthworms. Interestingly enough, most internal structures display a more or less

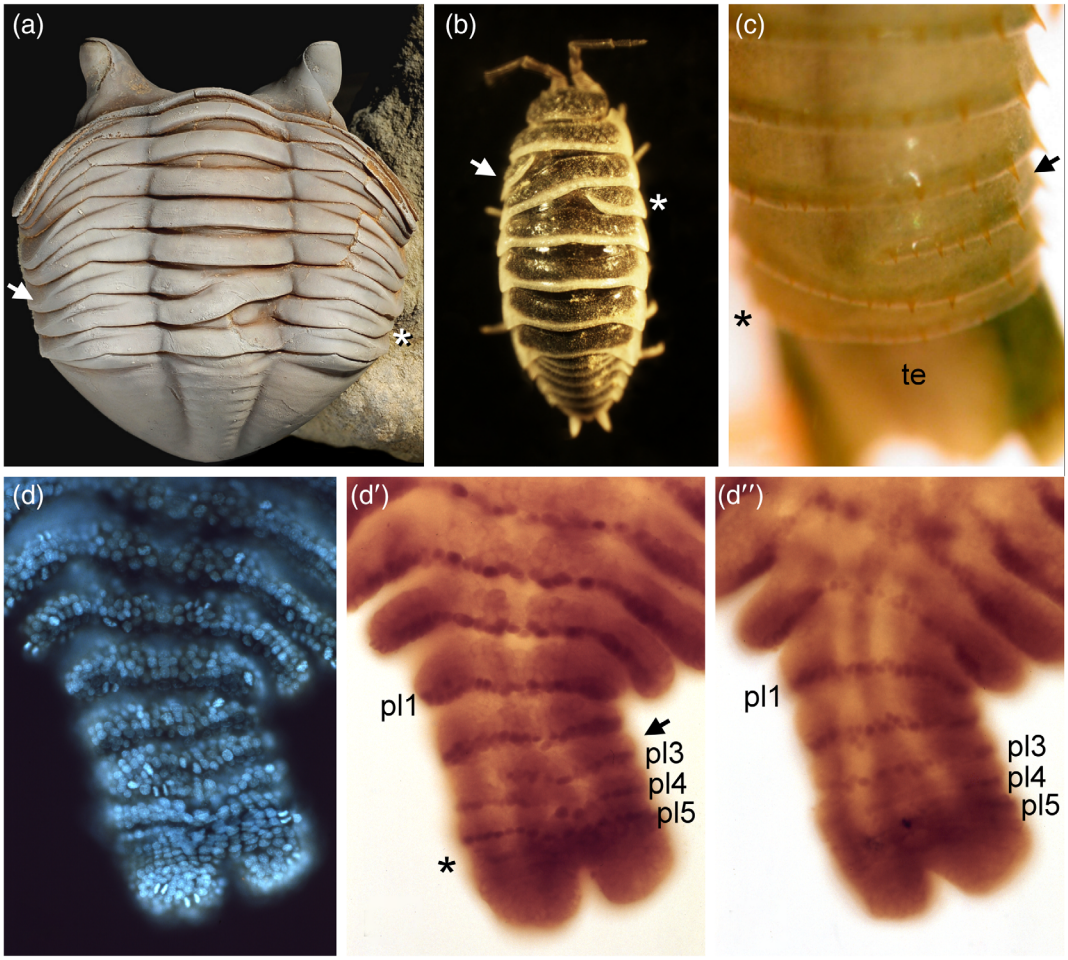

FIGURE 3 Further examples of spiral segments in arthropods. (a) The Ordovician trilobite *Asaphus punctatus* Lesnikova, 1949 showing a dorsal, right-handed spiral with one loop in the posterior thorax (photograph: Michael Zwanzig). (b) The isopod crustacean *Hemilepistus reaumuri* (H. Milne-Edwards, 1840) with a dorsal, right-handed spiral with one loop in the anterior thorax (photograph: Tzach Auman). (c) The notostracan crustacean *Triops cancriformis* (Bosc, 1801) with a one-looped, right-handed spiral in the posterior abdomen. It ends at the boundary of the telson (te) (photograph: Thorid Zierold). (d–d″) An artificially induced (cell ablation) ventral, left-handed spiral in the embryonic pleon of *Cherax destructor* Clark, 1936. (d) fluorescence staining of the cell nuclei showing the perturbation in the posterior region (ventral view of the germ band). (d′) Same perspective as in (d) as seen with light microscopy. The segment polarity gene *engrailed* is expressed in the posterior region of each forming segment (brown stripes). The spiral begins in the third pleon segment (pl3), there is only a half *engrailed* stripe in the animal's left side. After two loops, the spiral ends in the fifth pleon segment (pl5). (d″) Dorsal aspect (deeper focus) of the same region showing the regular engrailed stripes of the third to fifth pleon segments (pl3–pl5) (after Scholtz, 2020b). pl1, pl4: first and fourth pleon segments. In all images, the beginning of the spiral is marked with an arrow, the end with an asterisk

normal pattern with the exception that either the paired dorsal or ventral structures are out of register. Internally, only the dissepiments of the coelomic cavities of annelids show sometimes a spiral arrangement forming "a continuous body cavity (coelom) lying between the coils of the septum, and this cavity is continuous from the anterior to the posterior end of the spiral." (Morgan, 1895, p. 427). Linder (1952, p. 22) mentioned that the longitudinal muscles of the abdomen in notostracans with spiral segments are arranged in the same regular pattern as in unaffected segments. However, in one figure he shows a slight interruption of the muscle bands in the region of a beginning spiral (Linder, 1952, figure 4). In contrast to this, *Artemia* sp. larvae treated with mycophenolic acid not only displayed spiral outer segment boundaries in the abdomen, but also a twisted musculature (Hernandorena, 1993). Interestingly, Morgan (1895, p. 427f.) described some cases in annelids in which the spirals of the coelom do not correspond to those of the external structures. The inner spiral of the dissepiments can be shorter than the outer one of the annuli. Alternatively, the outer annuli show a spiral arrangement, whereas the internal region shows a normal pattern. Morgan (1895) concluded, therefore, that outer and inner segmental structures show a certain degree of morphological independence. In any case, further studies are required to clarify this issue.

4 | AT WHAT DEVELOPMENTAL STAGE ARE SPIRAL SEGMENTS GENERATED?

Most descriptions of helicomery are based on studies of adult specimens. A few reports deal with freshly hatched clitellate worms

(Morgan, 1895), insect larvae, and insect pupae (Lüscher, 1944; Balazuc, 1948; Benton & Jennings, 1975; Figures 1 and 2). There are only a few accounts describing insect and crustacean embryos with spiral segments (Chesebro, 2012; Scholtz, 2020b; Figure 3). In addition, some of the malformations of horseshoe crab embryos as shown in the plates of Patten's (1896, e.g., figures 13, 32) comprehensive study would probably have resulted in helicomery. These observations lead to the question: at what stage are spiral segments formed? Spiral segments as observed in annelids and arthropods most likely have a twofold origin: they form during embryonic or post-embryonic segment formation and during regeneration of adults after an injury (see Cori, 1892; Morgan, 1895; Sayles, 1936). The postembryonic addition of segments in anamorphic annelids and arthropods is comparable to embryonic segment addition (see Lans et al., 1993; Manzanares et al., 1993; Prud'homme et al., 2004; Scholtz & Dohle, 1996). In the case of adult regeneration, two different processes can be discriminated: (a) the regeneration within segments that were injured, and (b) the regeneration of complete segments after loss of parts of the trunk. The process of segment regeneration shows some similarities to embryogenesis, at least in annelids where regeneration of trunk segments occurs quite frequently (Bely & Wray, 2001; Zattara, 2020). In contrast to this, regeneration of lost segments in arthropods is rare (Maruzzo & Bortolin, 2013; Zattara, 2020). Hence, in arthropods one can predict that helicomery is based on embryonic and postembryonic segment formation, and on wound healing in adult segments. In annelids all possibilities occur. Yet, Morgan (1895) concluded that at least in annelids embryonic development results in a lower number of cases of helicomery than adult segment regeneration.

5 | WHAT CAUSES HELICOMERY?

As with other malformation patterns, numerous speculations and hypotheses have been proposed about the factors that may have caused the observed effects (see Scholtz, 2020a). These assumptions relate (a) to genetic mutations or (b) environmental impacts on (embryonic) development such as high temperature, radiation, chemicals, parasites, and (c) mechanical stress on developmental stage and adults, for example, pressure and lesions that lead to irregular wound healing and regeneration (see e.g., Balazuc, 1955, 1958). Salt (1927) reported spiral segments in aculeate hymenopterans that were infested by the parasitic strepsipteran insect *Stylops*.

However, as always, one has to clearly separate the levels at which the observed phenomenon's causes are explained. In the case of helicomery one can discriminate between mechanism at the genetic level, at the cellular level, and at the morphogenetic level. The mechanism that leads to a mismatch of segments can be chemical or mechanical. For instance, cell behavior can be intrinsically influenced by the misexpression of a protein (e.g., cadherins, see Tepass et al., 2000) or by an extrinsically applied chemical substance (e.g., cytochalasin B, see Itow & Sekiguchi, 1980). The misexpression of a protein can be caused by a change at the genetic level such as a natural or experimentally induced mutation (e.g., Schreader et al., 2010; Chesebro, 2012) or by an increased temperature.

Likewise, an injury-induced ablation of tissue leading to removal or a different arrangement of cells can have the same effect. These cellular changes may produce a topographical alteration in the spatial relationship of segmental primordial structures; in combination with regular developmental segmentation processes, this may end in a malformed pattern such as helicomery (Scholtz, 2020b). Most of the previously considered causes for helicomery centered on these morphogenetic aspects. Cori (1892) and Morgan (1892, 1895), for instance, discussed the origin of spiral segments in annelids due to irregular arrangement and sizes of the paired mesoderm blocks that are characteristic for annelid segmentation. Normally these blocks are of equal size and in exact pairwise register, resulting in proper integration of the two lateral halves of primordia in one segment and thus an orderly sequence of segments along the longitudinal body axis. If, according to Cori (1892) and Morgan (1892, 1895), this order is interrupted by larger, overlapping or smaller mesoderm blocks on one side, the forming segmental structures show a disarrangement which in some cases leads to a mismatch of segmental halves. Cori's and Morgan's views still may apply to developmental and regenerative segment formation, although the modern perspective on segmentation in annelids is somewhat more complex regarding the initiation of segment formation and the role of germ layers (Zattara & Weisblat, 2020). Furthermore, Cori's and Morgan's model does not really fit the mode of arthropod segmentation, where large mesodermal blocks do not occur during embryogenesis (Koch, Quast & Bartolomaeus, 2014). Cockayne (1929) proposed that a mismatch of tergites might be explained by an irregular dorsal closure during embryonic development in a number of insects. Based on an investigation of geophilomorph centipede segmental malformations including helicomery, Leśniewska et al. (2009, p. 423) suggested that helicomery may result from different developmental defects such as "pure dorsal mispairing, trunk shrinkage producing dorsal mispairing, and 'ventral mispairing'". This discrimination is based on the fact that in the arthropod germ band, the ventral side of the segments forms first, and only later the lateral and dorsal parts of segments differentiate. Accordingly, if a developmental effect occurs at the early germ band stage, it results in a ventral mispairing and if the defect involves the later dorsal closure, it leads to a dorsal mispairing. Another potential cause for ventral mispairing of segment primordia might be an irregular ventral closure of germ bands. A ventral closure occurs in citellate annelids, in which the lateral germ band halves are dorsally formed followed by a fusion at the ventral side (Anderson, 1973; Zattara & Weisblat, 2020). Similarly, arthropods such a arachnids, chilopods and some crustaceans undergo a temporary split of the germ band that subsequently reconnects ventrally (e.g., Anderson, 1973; Gerberding & Scholtz, 1999; Chipman, Arthur & Akam, 2004; Schwager; Schönauer, Leite, Sharma & McGregor, 2015).

The molecular genetic causes for helicomery have rarely been studied, and only in insects. Sobels (1952) investigated *Drosophila melanogaster* mutants with segmental deformations. He analyzed the abdominal phenotypes of pupae and adults and found a variety of abnormal segmentation patterns including spiral segments. He identified a potential polygene factor, which he called "Abnormal abdomen" as being linked to the helicomery phenotypes (Sobels, 1952).

However, the concrete mechanism of how "Abnormal abdomen" creates spiral segments was left open.

6 | EXPERIMENTAL APPROACHES

There are some experimental approaches that have led to spiral segments. The ablation of anterior segments in a polychaete resulted in a regenerated part with two areas of helicomery (Sayles, 1936). Balazuc (1955) induced helicomery in a mantid by mechanical stimulation (vibrations) of the egg case. Nevertheless, these experiments did not reveal the morphogenetic process that may lead to the observed helicomery. All that can be said is that regeneration of segments is correlated with more irregularities, including helicomery, than normal segment generation during development. This has already been suggested by Morgan (1895) based on his comparative analysis of lumbricid malformations. Experiments that directly affect cell division and cell death provide a better clue to helicomery, even if they do not focus on developmental segment formation. Spiral segments were observed in larval and adult moths (*Tineola bisselliella* [Hummel, 1823]) after UV-radiation of eggs and embryos (Lüscher, 1944). An exposure of opilionid eggs to increased temperatures resulted in some examples of helicomery among other malformation patterns (Juberthie, 1968). In the crustacean *Artemia* sp., spiral segments were produced in the abdomen based on an experimental treatment with mycophenolic acid, which has a cytostatic effect (Hernandorena, 1993). The generation of null-mutants for the *morgue* gene in *Drosophila* led, among other effects, to spiral segments in the abdomen of adult flies (Schreader et al., 2010). Since the morgue protein plays a crucial role for the regulation of cell death, its absence in null-mutants affects cell proliferation. Chesebro (2012) carried out RNAi experiments with the gene *tarsal-less* in the cockroach *Periplaneta Americana* (Linnaeus, 1758). These led to abnormal segmentation patterns in the abdomen, among them some resembling spiral segments. In addition to other functions, Chesebro (2012) identified a role of the *tarsal-less* gene for anterior and posterior body patterning. Suppressed expression of the gene leads to misaligned segmentation between left and right body halves and the fusion of segments (Chesebro, 2012).

A series of cell ablation experiments in the embryonic germ band of the Australian crayfish species *Cherax destructor* Clark, 1936 resulted in a number of different morphological patterns, cell arrangements, and the expression of the segment-polarity gene *engrailed* (Scholtz, 2020b). Among these patterns, a case of helicomery that is particularly interesting concerns a spiral circumscribing the forming third to fifth pleon segments (Figure 3d–d″). Not only is the cellular arrangement spiral, but also the stripe of monoclonal *engrailed* antibody labeling forms a clear spiral (Figure 3d′, d″). Since *engrailed* is normally expressed in the posterior region of forming arthropod segments (see Patel, Kornberg & Goodman, 1989; Scholtz, Patel & Dohle, 1994; Damen, 2002; Hughes & Kaufman, 2002), the spiral arrangement indicates that a shift of cells leads to a subsequent spiral formation of segments that is reflected at the molecular level.

7 | THE LABYRINTH-MODEL OF HELICOMERY

The labyrinth of the medieval Basilica of St. Quentin in France (see Gailhabaud, 1858) can serve as a model for how relatively few changes in a serial pattern can dissolve seriality (Figure 4). This pavement labyrinth was created around 1495 and it follows a long cultural tradition of labyrinths and mazes (Kern, 2000; Kürvers & Niedermeier, 2006). It has a hexagonal shape and it measures around 11.66 meters in width. In reality, the tiles are somewhat irregular in

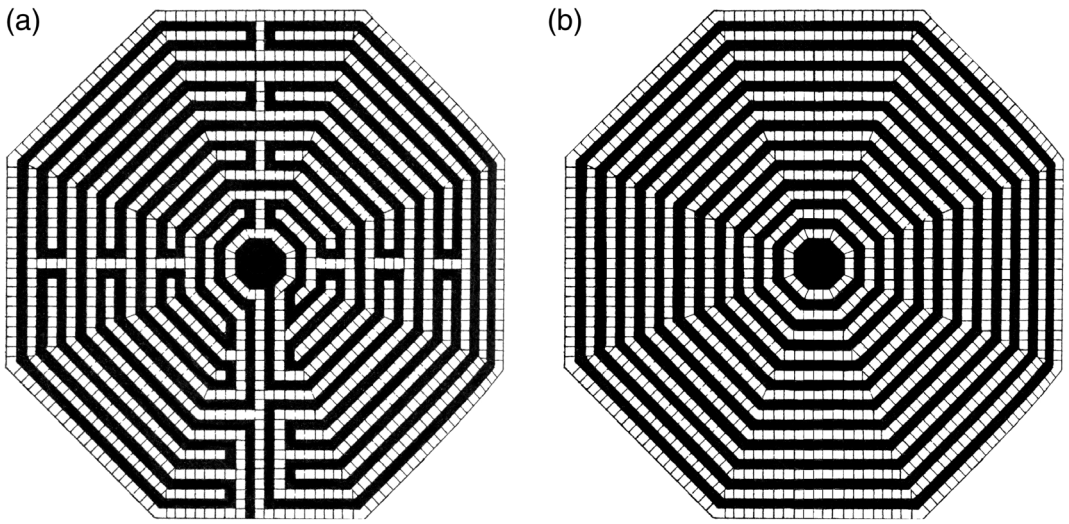

FIGURE 4 The labyrinth of the medieval basilica of St. Quentin, France. (a) The idealized labyrinth forming a complicated spiral of the black line leading from the margin to the center. (b) The regular ground form of concentric hexagonal lines of black and white tiles. Only a few changes are required to switch from simple concentric lines to the complicated spiral. This serves as a model for the change from serial structures to spirally arranged structures (modified after Gailhabaud, 1858 and Möller-Fernau, 1932). For details, see text

size. Yet, following the idealized graphic representation of Gailhabaud (1858) the labyrinth consists of 2200 black and white tiles which are arranged in 11 black and 12 white lines and a black center (Möller-Fernau, 1932) (Figure 4a). Pilgrims are supposed to walk along the black line forming a spiral zigzag course to the center. The entire path is 853 meters (Möller-Fernau, 1932). The complicated structure of the black path can be derived from a regular arrangement of 12 white and 11 black concentric hexagonal lines and a black center (Möller-Fernau, 1932) (Figure 4b). Only 47 white tiles have to be exchanged for black ones to achieve the complex structure of the labyrinth (Möller-Fernau, 1932). If the regular original arrangement is considered as a planar projection of serially arranged structures such as segments, then the little changes necessary to derive the labyrinth resemble the situation of the creation of spiral segmentation.

7.1 | Translating the labyrinth into three-dimensions

An explanation of the formation of helicomery has to deal with three aspects: one is the beginning of the spiral, the second is the continuation, and the third is its ending. In cases of a simultaneous generation of segments, as in long gem insects like *Drosophila*, and within a field of differentiated segments, the three aspects of spiral segment formation: begin, continuation, and end are combined in one step and the spiral does not grow longer (Figure 5c). This is different in short germ insects, most other arthropods, and annelids where segments are generated sequentially along the anteroposterior. Here, begin, continuation, and ending of the spiral are three subsequent processes (Figure 5d).

In any case, the starting point for the formation of spiral segments is an irregular positional change of cells after the segmental boundaries have been determined (Figure 5). This can occur in an early embryo, a larva, or an adult animal. It can be an injury that leads to the detachment of a slightly obliquely piece of tissue (Figure 8b). Alternatively, an altered cell state determination, a different cell adhesion property, suppression of normal cell division activity, and cell death can have the same effect. The "lesion" should span at least the length of one segment or its primordium in an anteroposterior direction (Figure 5b). For instance, in malacostracan crustacean embryos, in which the stereotyped cell lineage of segments has been followed in great detail (Scholtz, 2020b), a shift of the length of one cell would be enough to initiate a spiral (see Figure 6). Something similar is true for segment formation in clitellate annelids (Weisblat & Winchell, 2020). The rearrangement of cells must lead to a situation, in which the two open ends of at least two adjacent segments lie closer together than the two other open ends. During tissue regeneration, this may result in the fusion of the closer open segment ends, whereas the more distant open ends do not show a fusion with a contralateral counterpart. The resulting pattern is a spiral turn with two open ends. If more than two segments or their primordia are affected, the spiral will be longer. Depending on the direction of the obliqueness of the injury, the spiral can be oriented clockwise or counterclockwise. If the initial spiral is situated directly anterior to forming segments, then there is the chance that the posterior open end of the spiral fuses with the margin of the adjacent newly forming segment (Figure 5d). This may be possible, because segments in arthropods and annelids differentiate from the ventral midline toward lateral and dorsal (Figure 6).

Once the spiral has been started, it provides no real challenge to segment formation and differentiation. On the contrary, segmentation processes in terms of gene expression, cell differentiation, segment addition, and ventro-dorsal growth and closure of the segment primordia can be employed in a normal way to create spiral segments. Each cell can maintain the same coordinates with respect to segment boundaries as in normal segments (see Meinhardt, 1986, 2008). According to Meinhardt (1986, 2008), a sequence of at least three different cell states is required to generate segmental boundaries, which

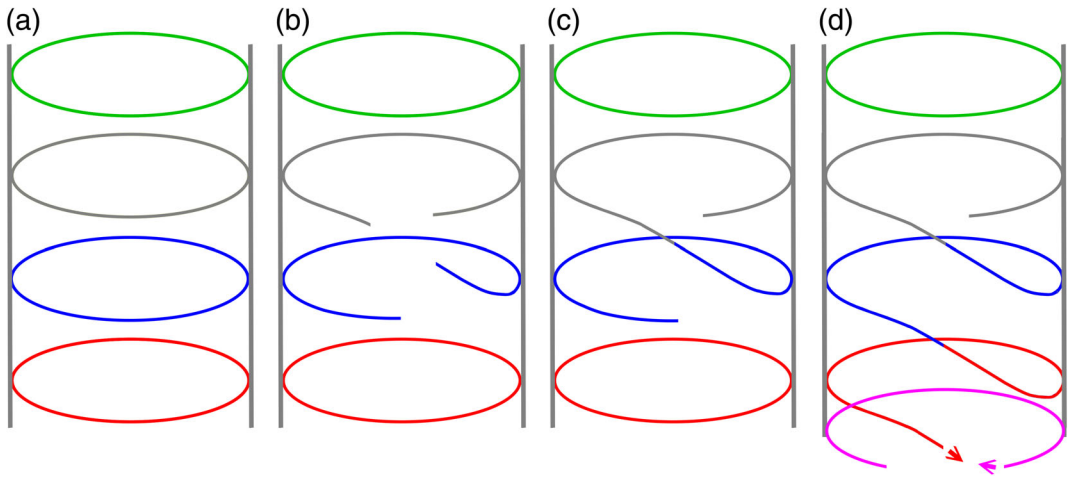

FIGURE 5 Model of the formation of spirals, dorsal view. The colored rings represent boundaries of serial structures. (a) The normal arrangement of serial structures along the longitudinal body axis. (b) An injury or another reason for a shift of cells (see text) affects two subsequent serial structures. (c) The shifted open ends grow together forming a one-looped spiral. The other ends remain open. The other serial structures remain in their normal shape. (d) If the cell shift happens in the area of formation of serial structures, the open ends of each newly forming serial structures (purple line) fuse to the wrong counterpart (red line) during dorsal closure (arrows). This way the spiral continues

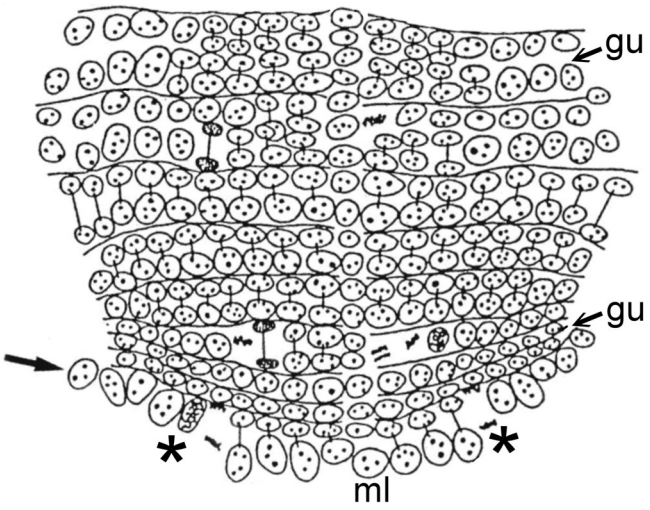

FIGURE 6 Posterior end of a germ band of *Neomysis integer* (Leach, 1814), ventral view (after Scholtz, 1984). The nuclei (with nucleoli) of ectoderm cells are shown. Sister nuclei are connected with a line. The ectoderm cells are budded by large stem cells called ectoteloblasts (left arrow) via a mediolateral wave of division left and right of the midline (ml), which forms a column of unpaired cells along the longitudinal body axis. Each ectoteloblast descendant row forms a genealogical unit (slim right arrows, gu), which are marked by horizontal lines. Two of these genealogical units contribute to a morphological segment in a more advanced stage (see Dohle & Scholtz, 1988; Scholtz & Dohle, 1996). Each genealogical unit increases in width trough two mediolateral waves of divisions, leading to width of four cells. Since the germ band shows an anterio-posterior developmental gradient, the more anterior genealogical units show different grades of advanced development. The lateral halves show a certain temporal independence in their development. In this case, the animal's right side is slightly in advance to the left side. The wave of division of the ectoteloblasts has reached six cells on the animal's right side (left asterisk) and only four cells on the animal's left side (right asterisk). Corresponding differences occur in the genealogical units. These differences may lead to a dorsal mismatch and thus a dorsal spiral, when the lateral sides propagate and form the dorsal closure. On the other hand, a slight shift between the right and left body half of a newly formed genealogical unit consisting of one cell row would be sufficient to create the beginning of a ventral spiral

are arranged as three subsequent cell rows in each segmental unit. Gene expression and cell states sensu Meinhardt (1986, 2008) can be the same as in normal segments. Likewise, the ventral dorsal boundary marked by the gene decapentaplegic remains in its normal position and the limbs are formed normally. If the positional shift of segmental primordia occurs on the ventral side, the dorsal closure follows a normal pattern, since two segments grow together in the area of the dorsal midline as in unaffected segments. On the other hand, a slight rearrangement of cells during dorsal closure can lead to a dorsal mismatch, which results in a dorsal spiral. In *Drosophila* embryos, this kind of mismatch of cells and tissues occurs during dorsal closure (e.g., Jacinto et al., 2000). In malacostracan crustaceans, the two lateral halves of the forming germ band show a certain independence with respect to their differentiation process (Dohle & Scholtz, 1988; Figure 6). The development of one half can be slightly in advance showing more cells than the other half and this can lead to a ventral or dorsal mismatch during segment formation if cells meet that normally would not.

The end of the spiral is more difficult to explain. Short spirals just seem to be affected at both ends by the length of the injury. Yet, this is unlikely for longer spirals, because such a long wound would probably not show such a regular spiral healing pattern. Furthermore, in cases in which the spiral is forming during embryonic or larval segment addition, the formation of the final half circle that ends the spiral is difficult to comprehend. If the spiral terminates at the anterior margin of the telson or the pygidium as has been found in crustaceans, myriapods, and hexapods (Balazuc & Schubart, 1962; Hernandorena, 1993; Linder, 1947; Morgan, 1895; Šaganović et al., 2019; Sobels, 1952), then the explanation would be that the spiral terminates at the proliferation zone and that telson and annelid pygidium are not segmental structures. A more anterior ending may be explained with an increasing irregularity of segment formation, which in the case of helicomery leads to an end of the spiral. Another possibility is that the gradient of spatiotemporal independence between the two germ band halves is less pronounced than in the area of the beginning spiral. This would lead to the situation that ventral or dorsal cells meet their regular counterpart and segmentation continues normally. However, the question of how spirals are terminated requires further studies.

The mechanism of formation of the spiral explains why, in the case of helicomery, the number of segmental structures such as limbs or ganglia are often not affected and thus, are the same in the two body halves (Figures 1-3). The only difference is that the whole segmental system is slightly oblique with respect to the body axis. The regularity of spiral segmentation processes is also supported by the normal differentiation of segmental morphological structures such as limbs and ganglia in annelids and arthropods and nephridia in annelids (Morgan, 1895). Only internal structures that are directly morphologically associated with segmental boundaries are affected, such as the dissepiments of the segmental coeloms in annelids (Morgan, 1895). These frequently occur in a spiral or screwed manner following the intersegmental furrows (Morgan, 1895).

8 | NON-SEGMENTAL SERIAL STRUCTURES OF ANNELID AND ARTHROPOD TRUNKS AND APPENDAGES

In the vast majority of cases, helicomery has been reported in trunk segments. Yet, it also occurs in other serial trunk structures such as the secondary annuli of leeches (Morgan, 1895; Figure 1e,e′). These annuli are superimposed on trunk segmentation but do not correspond to segments and their boundaries. The diplosegments of diplopods combine an outer annulus with two pairs of limbs and other double segmental structures (Figure 2e). Diplosegments are the result of the fusion of two adjacent dorsal segmental units during late embryonic development (Janssen, 2011). Interestingly, all reported

spirals in diplopods follow the margins of the diplosegments and do not separate the two pairs of limbs (Balazuc & Schubart, 1962). This suggests that the spirals in diplopods formed after dorsal fusion of two segmental units. In addition to these trunk spirals, helicomery has been described for annulated arthropod appendages like the first and second antennae of a lobster, the antennae of a cockroach, of two beetle species, and the pleopods of an amphipod (Morgan, 1895; Arendsen Hein, 1924; Asiain & Márquez, 2009; Maruzzo & Minelli, 2011; Figure 7).

9 | HELICOMERY IN OTHER TAXA WITH SERIAL STRUCTURES ALONG THE ANTEROPOSTERIOR BODY AXIS

Helicomery of the trunk is not restricted to animals with outer body rings marking segmentation. Axial serial structures occur in many of the major bilaterian groups (Vellutini, 2020). Hence, it seems reasonable to look for spirals in non-segmented animals (Figures 8,9).

Similar phenomena to those reported above have been described for several species of cestodes, in which the proglottids sometimes show asymmetries and spiral patterns in a similar fashion to those found in annelids and arthropods (Brandes, 1899; Child, 1900; Grohmann, 1906; Figure 8).

There is one description of malformations in the vertebrae of the amphibian species *Triturus dobrogicus* that might be a case of helicomery. Buckley et al. (2013) described a characteristic pattern with additional ribs that are arranged in an alternating mode. The fused vertebrae show somewhat oblique contact zones, again in an alternating pattern. The resulting overall appearance suggests a corresponding mechanism to that found in annelids, arthropods, and cestodes despite the fact that vertebrate segmentation is not expressed in outer annuli (Figure 9).

A number of nematode species (e.g., of the Desmoscolecidae, Criconematidae, and Desmodoridea) show superficial cuticular rings. These are not related to other serial structures of the body. In some cases, these rings are irregularly formed and a spiral arrangement can be deduced from the figures of the publications of, for example, Decraemer (1985), Figures 1, 6, and 7), Urbancik et al. (1996),

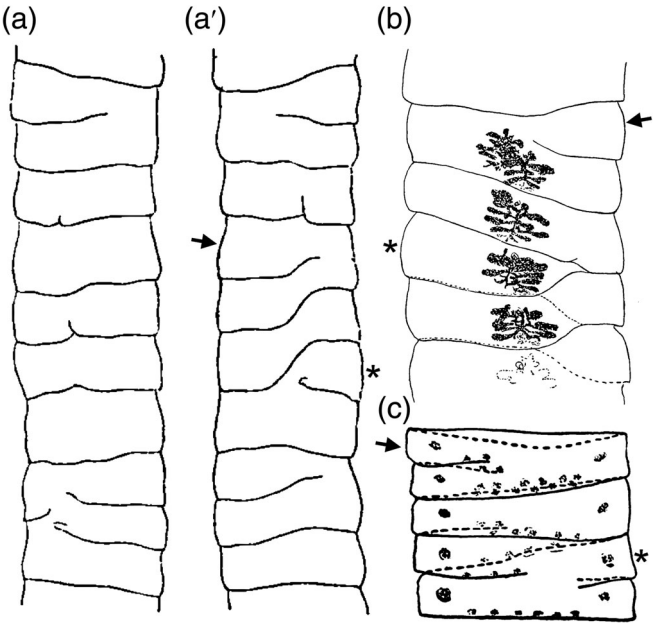

FIGURE 8 Spirals in Cestodes. (a, a′) Two sides of the tapeworm *Taenia saginata* Goeze, 1782 one right-handed spiral, (after Brandes, 1899) (b) The tapeworm *Diphyllobothrium latum* (Linnaeus, 1758), ventral view, left-handed spiral (after Grohmann, 1906). (c) The tapeworm *Moniezia expansa* Rudolphi, 1810 ventral view, right-handed spiral (after Child, 1900). In all images, the beginning of the spiral is marked with an arrow, the end with an asterisk

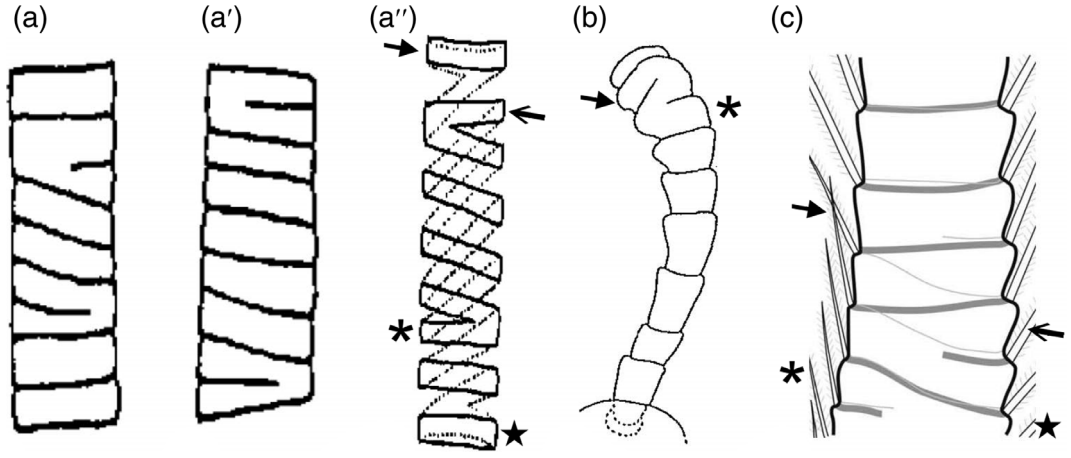

FIGURE 7 Spirals in arthropod appendages. (a, a′, a″) "Crustacea": Two sides and scheme of spirals in the annuli of the second antennae of the decapod *Homarus americanus* Milne Edwards, 1837, two spirals: One in other, both left-handed (after, Morgan, 1895). (b). Hexapoda: Antenna of *Tenebrio molitor* with a right-handed spiral (after Arendsen Hein, 1924). (c). "Crustacea": Pleopodal exopod ramus of the amphipod *Gammarus roeselii* Gervais, 1835 with two left-handed spirals (after Maruzzo & Minelli, 2011, with permission from Elsevier). In all images, the beginning of the spiral is marked with an arrow, the end with an asterisk. If there are two spirals, the beginning of the second spiral is marked with a slim arrow and the end with a star

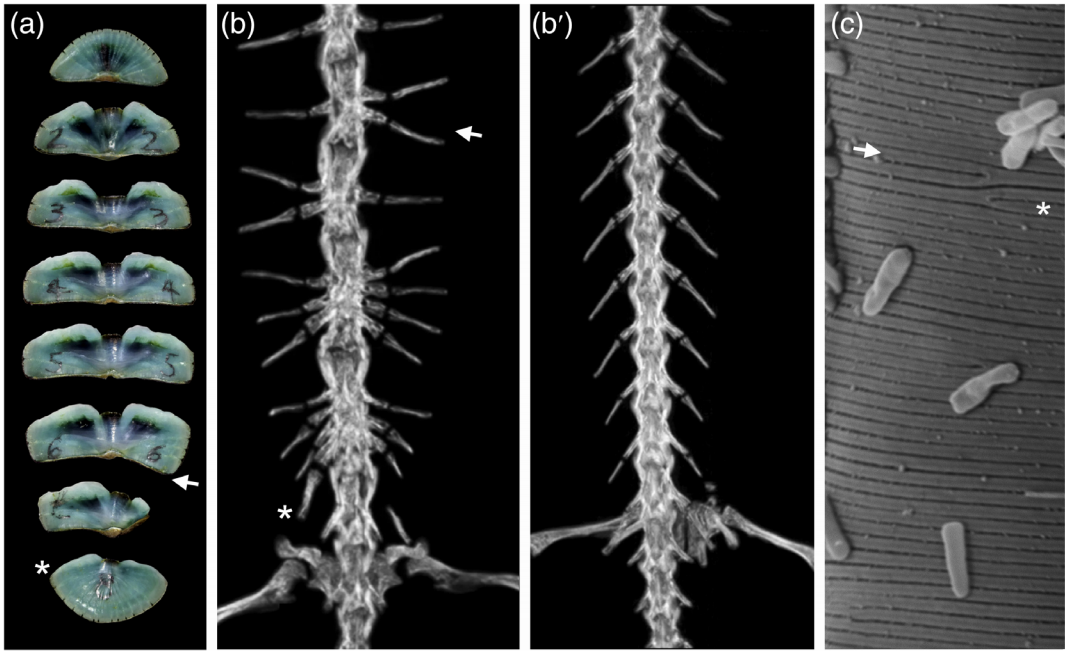

FIGURE 9 Putative spirals in other taxa. (a) The mollusk *Chiton articulatus* Sowerby, 1832 ventral view of shell plates, shell Plate 6 has additional silts on the animal's left side, Plate 7 is reduced at the left side and Plate 8 is slightly larger on the animal's right side. This may indicate a spiral, but the serial structures on the ventral side of the soft parts of the body have to be studied (after Avila-Poveda et al., 2019, with permission from Elsevier). (b,b′) The vertebrae of the newt *Triturus dobrogicus* (Kiritzescu, 1903) the malformed specimen B shows oblique vertebrae boundaries and a left, right alternating number of ribs indicating a spiral pattern, (b′) A normally developed specimen of the same species (after Buckley et al., 2013). (c) The nematode *Robbea hypermnestra* Ott et al., 2014 showing a putative spiral with two loops (photograph: Nikolaus Leisch). In all images, the beginning of the spiral is marked with an arrow, the end with an asterisk. If there are two spirals, the beginning of the second spiral is marked with a slim arrow and the end with a star

Figure 1), Hoschitz, Buchholz & Ott (1999, figures 19, 20, 29), Karssen and van Aelst (2002), Figure 3), Powers et al. (2016), Figure 7), and Maria et al. (2020), Figure 7) (see Figure 9c).

The last example is somewhat weaker and a question mark has to be added. This instance concerns the polyplacophoran *Chiton articulatus* Sowerby, 1832. In several specimens, aberrations of the dorsal shell plates have been found that at first sight resemble segmental aberrations as described for annelids and arthropods (Avila-Poveda et al., 2019). These concern asymmetries in fusion und fission and plates that are covering only one body half. Yet, before one can speculate about a spiral pattern, more detailed data about the arrangement of serial structures of the ventral side of these specimens are necessary. As in vertebrates, spirality would not be expressed in outer body rings. If it occurs, it rather concerns the topographical relationships of the malformed shell plates to the serial ventral attachment sites of dorsoventral muscles, serial gills, and so forth (see Götting, 1974). Hence, the problem of helicomery in mollusks currently remains unsolved (Figure 9a).

10 | IS HELICOMERY A DISTINCT CLASS OF MALFORMATION?

Following a process-oriented approach, Leśniewska et al. (2009) concluded that helicomery should not be treated as a class of anomalies in its own right, because these authors inferred different causes for the various anomalous patterns that they observed in the centipede *Stigmatogaster subterranea*. Indeed, from what I have listed above, one can assume that there are different stimuli that may lead to helicomery. However, a change of the normal cell arrangement of segments or other serial units is always involved. Moreover, helicomery is characterized by a distinct structural pattern: it implies serial structures bridging two directly adjacent serial units. In other words, what makes helicomery specific is the pattern not the process. Hence, it is justified to consider helicomery as a distinct class of anomalies.

11 | THE MEANING OF HELICOMERY FOR THE CONCEPT OF SEGMENTATION

Helicomery reveals an interesting aspect concerning our view of segments and segmentation. Generally, segments are conceptualized as units that are serially arranged along the anteroposterior-body axis (Scholtz, 2002, 2020c). Likewise, the parts that constitute a segment such as ganglia, legs, nephridia, and the outer annulus are serially arranged structures. This serially arrangement is fundamentally destroyed by the helicomerous pattern (Figure 10). Legs that are normally paired structures of the left and right body halves and hence repeated as series of leg pairs, are now individual, unpaired legs that form a serial sequence on a spiral along the body axis (Figure 10). The

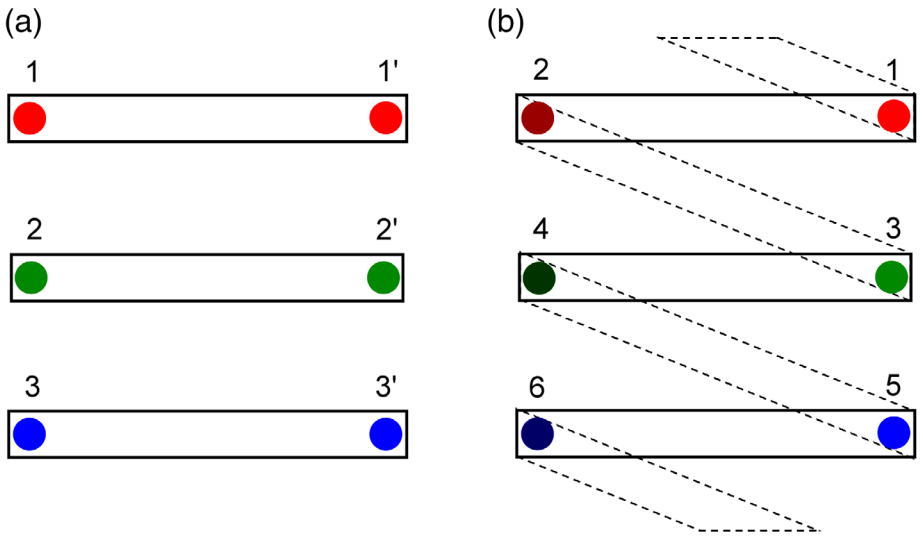

FIGURE 10 Helicomery dissolves segmentation. (a) the normal arrangement of segmental structures as a series along the longitudinal body axis. The colored dots represent the paired serially arranged segmental structures such as appendages, ganglia, and so forth. The numbers show the serial (1, 2, 3) and bilateral (1, 1′ etc.) arrangement. (b) segmentation is dissolved due to helicomery and the former segments form a continuous band. The serial segmental and paired bilateral arrangements of structures are replaced by a series on a three-dimensional spiral (different shading of dots and numbers 1–6)

integrity of the segments is thus eliminated. Strictly speaking, the body in the helicomerous regions is not segmented, and thus, helicomery dissolves segmentation (see Fusco et al., 2008; Scholtz, 2020c). At a more abstract level, a translational symmetry is transformed into a spiral symmetry. Translational symmetry is characterized by identical serial elements that are translated into one another by a shift along the axis, whereas three-dimensional spiral symmetry is a curve that constantly turns around an axis, which implies a mirror asymmetry (Tarassow, 1999).

12 | A COMMON PRINCIPLE UNDERLYING SERIALITY IN BILATERIANS?

Helicomery appears in a variety of axial serial structures that show no shared similarity apart from the seriality itself, irrespective of whether these are conceptualized as segments or not (see Minelli, 2020; Scholtz, 2010, 2020c). Based on current ideas of bilaterian phylogeny, it is likely that these serial structures evolved independently (see Scholtz, 2020c; Vellutini, 2020). Moreover, helicomery occurs despite fundamental differences in the ontogeny of axial serial structures. This is already true for segment formation of arthropods and annelids. Long germ-band insects such as *Drosophila* as well as short germ-band insects and other arthropods such as grasshoppers, isopod crustaceans, myriapods, and chelicerates show similar patterns. Corresponding cases of helicomery are also found in animals with anamorphic development such as most annelids, trilobites, notostracan crustaceans, and diplopod myriapods, and in those with epimorphic development such as pterygote insects and geophilomorph centipedes. Furthermore, despite similar patterns of helicomery, segmentation processes of annelids, arthropods, and chordates are quite different at the molecular level (Chipman, 2020). Likewise, the formation of the serial podomeres of arthropod appendages differs from segment formation in the arthropod body (Jokusch, 2017).

These ontogenetic differences are even greater when serial structures of non-segmented animals are considered. For instance, proglottids lack the set of characters that has been used to define segments (see Scholtz, 2002, 2010, 2020c). Furthermore, proglottids do not form by a combination of a pre-anal proliferation zone and an anteroposterior differentiation of segments, but rather by stem cells that form a growth zone in the neck area behind the anterior scolex; the differentiation follows a posteroanterior gradient (Koziol et al., 2016; Olson, 2008; Rozario et al., 2019). Likewise, the formation of the cuticular annuli in nematodes follows a different pathway compared with annelids and arthropods. In *Caenorhabditis elegans* (Maupas, 1900), the superficial cuticular annuli are generated simultaneously during the elongation of the embryo; this occurs in an extracellular layer produced by epidermal cells which contain serially arranged filamentous actin bundles (Priess & Hirsh, 1986).

This widespread occurrence of helicomery in different structures of diverse animal groups strongly suggests that it affects the formation of serially repeated axial structures in general, irrespective of their differing morphologies and ontogenies. In other words, the formation of a spiral pattern of axial serial structures in distantly related metazoan groups and in different body parts indicates a general principle of seriality that is destroyed by helicomery. Hence, helicomery creates indirect evidence for a common principle of axial seriality in bilaterians or animals in general. This common principle is independent of the homology of the structures, and is likely to be independent of the various molecules of the signaling pathways leading to the formation of the different serial structures. Hence, it does not relate to concepts such as "Turing self-organization" (Metz et al., 2011), "co-option of genes" (True & Carroll, 2002), "deep homology" (Shubin et al., 2009) and "emergent properties of the circuitry and the spatial arrangement of signaling pathways" (Held Jr. & Sessions, 2019). The general principle that I suggest means that iterated units along an axis share some inherent morphological structural properties. The nature of these properties needs to be determined.

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Gerhard Scholtz: Conceptualization; visualization; writing-review & editing.

CONFLICT OF INTEREST

The author declares no conflict of interests.

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